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A Contribution to the Anatomy of the Human Retina, with a Special Consideration of the Terminal Loops of the Rods and Cones.

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A CONTRIBUTION TO THE ANATOMY OF THE HUMAN
RETINA, WITH A SPECIAL CONSIDERATION OF THE
TERMINAL LOOPS OF THE RODS AND CONES.

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AND

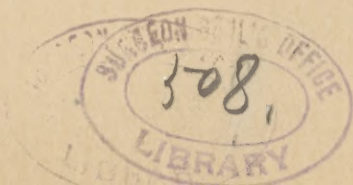
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THE anatomy of the rods and cones of the human retina is confessedly a difficult field of research. These delicate organs rapidly undergo change after death, and during life they are often altered by disease; moreover, they are easily swollen or shrunken in the process of preparation by the menstrua and reagents employed. An opportunity to study them to advantage by modern methods with immersion lenses is thus very rarely obtained, and as a consequence anatomists have often been obliged to resort to the lower animals for much of the material of their investigations. The structures that have been figured in the retina have usually been observed in the eyes of fishes, frogs, crabs, birds, and some mammals. These animals can be easily killed and the retina at once fixed; but we can only remove diseased human eyes from the living body, and even after death a decent interval of time must be allowed to elapse before the eyes can be examined. The nearest approach to a normal condition of the retina would thus seem to be afforded by such a wound of the eye as justified its immediate enucleation.

The eye which furnished the specimens from which our illustrations have been made was wounded by a scale of iron which passed through the cornea, lens, and vitreous, and was found embedded in the sclerotic. The eyeball was enucleated and immediately placed in Müller's fluid; subsequently stained with carmine and embedded in paraffin.

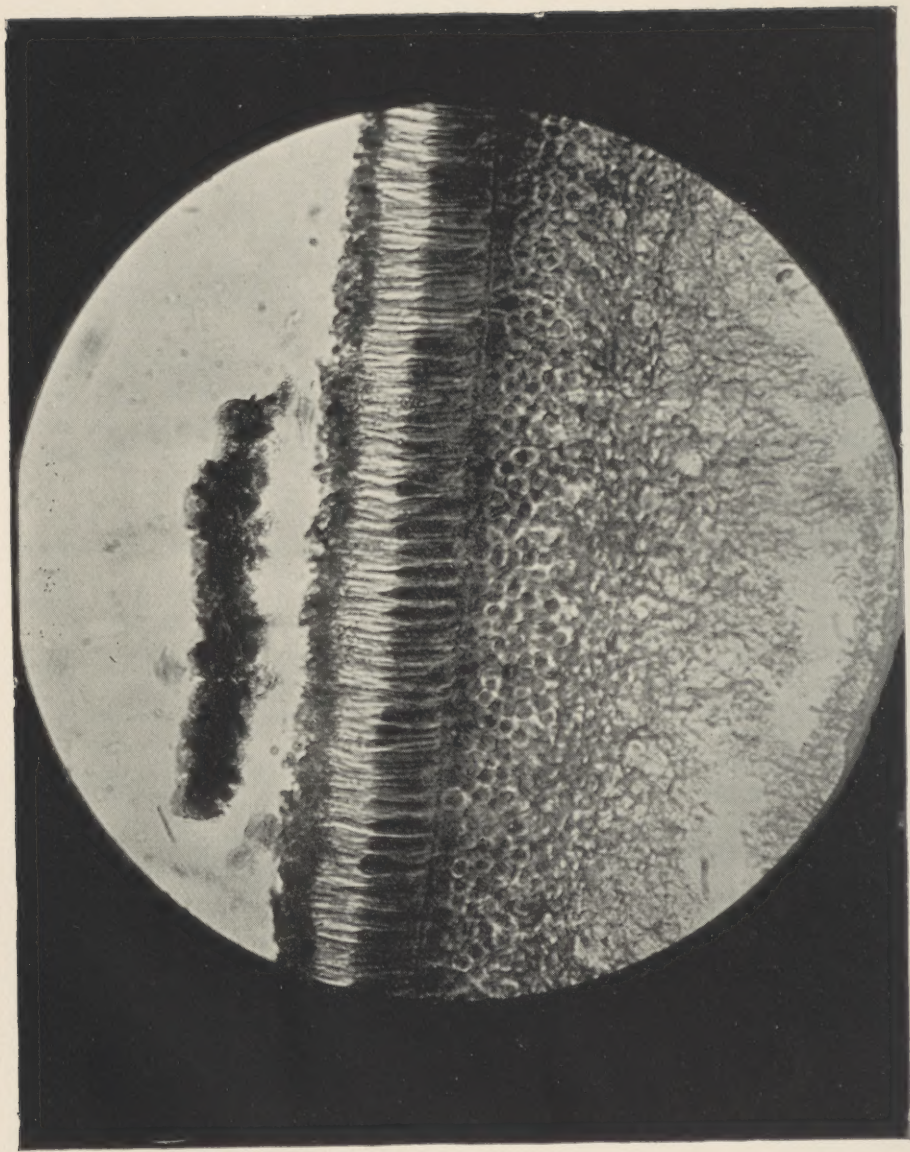
Of the many careful and laborious researches into the anatomy



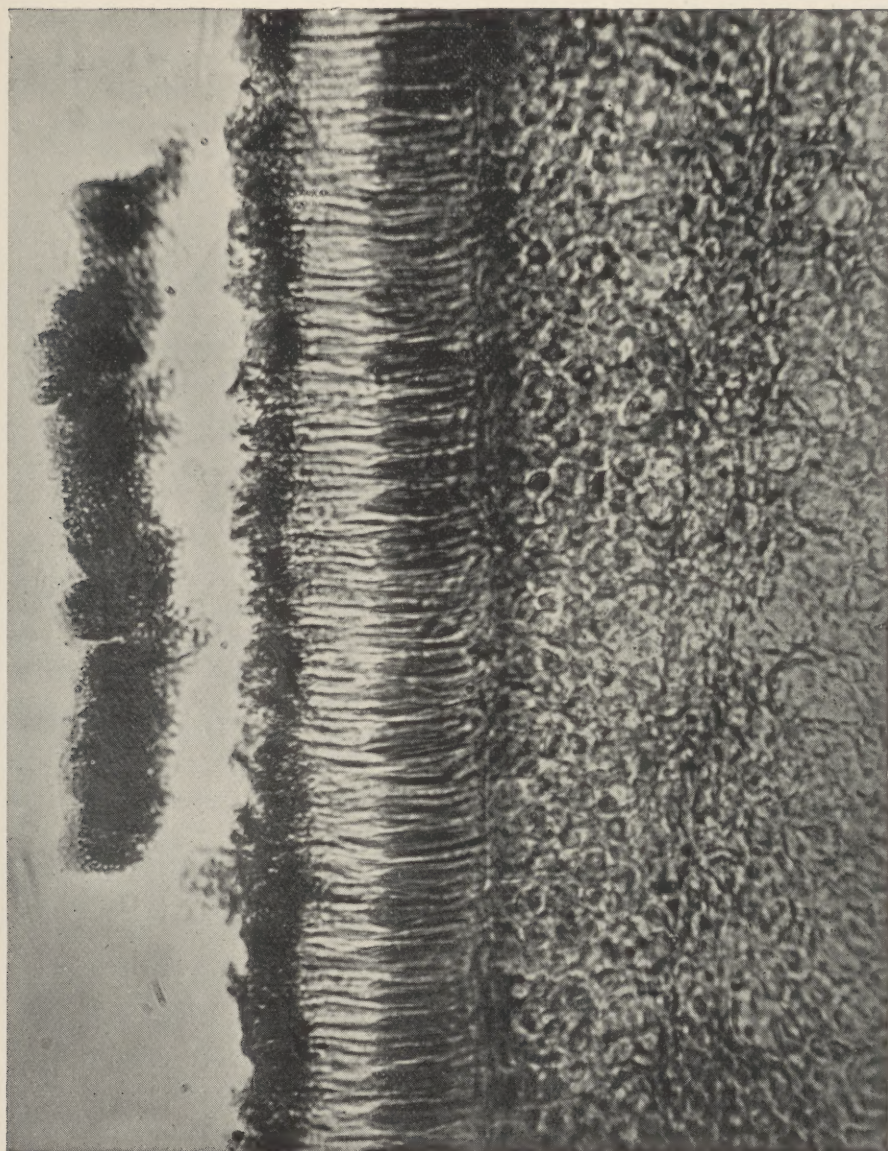
of the retina, those of Henle, Heinrich Müller, Max Schultze, and Hannover stand out prominently. According to Schultze, "Heinrich Müller discovered in the retina radial fibres passing through its various layers, and the accurate deductions which Kölliker and Müller associated with this discovery, procured a ready and general acceptance of the opinion that the rods and cones are the ultimate terminations of the fibres of the optic nerve, and are therefore the percipient elements of the retina. In fact, the anatomical relations of the retina allow no other explanation of the mechanism of the visual act. On the surface which receives a distinct image of outside objects there is required a definite number of these sensitive points. The greater the number of these sensitive points there is in a given space, the more acute will be the perception of form. What arrangement could be more suited to this object than that of the layer of rods and cones whose ends constitute a mosaic of elements, each forming an independently sensitive area, small enough to explain the acuity of vision as it is observed in human beings? We have sufficient grounds for the assumption that every sensation originates primarily in a nerve-end. That such nerve-ends do not exist in the fibre layer is beyond doubt. The layer of ganglion-cells offers no ground for the theory of the nerve-endings being contained there. They can only be regarded as a medium for the transmission of the nerve-fibres. The discovery by Heinrich Müller of the radiating fibres extending to the cones and on to them showed the route by which the impressions were conveyed from the cones to the optic nerve. Purkinje's experiments demonstrating that the eye could perceive the shadows of its own retinal blood-vessels, proved that only the outer layers of the retina could be the percipient ones, since the blood-vessels reach to the outer granular layer, and there only remain the outer nuclear layer and the layer of rods and cones. Müller demonstrated the connection between the outer nuclear layer and the layer of rods and cones. The rods and cones, or both together, must, therefore, be the percipient elements."¹ From Kölliker we quote the following: "Hannover, the first who has systematically discussed the cones of the retina, did not extend his investigations to human beings, and only describes the cones in the mammalia as long round bodies one-half the length of the rods, with two very short round points on their outer end. Best of all have Pacini and Henle treated the subject. Pacini describes them as conical or pear-shaped bodies .0156 mm. in length and .0093 mm. in breadth, which sometimes are single and sometimes are connected to another cone (twin cones), or appear to be connected with a rod. He further asserts that the outer end of the rod bends on itself and becomes connected with the end of a cone."² Hannover's most recent work (1876),

¹ Schultze: *Anatomie und Physiologie der Retina*, Bonn, 1866, pp. 2, 3.

² Kölliker in H. Müller's *Gesammelte und Hinterlassene Schriften*, Leipzig, 872.



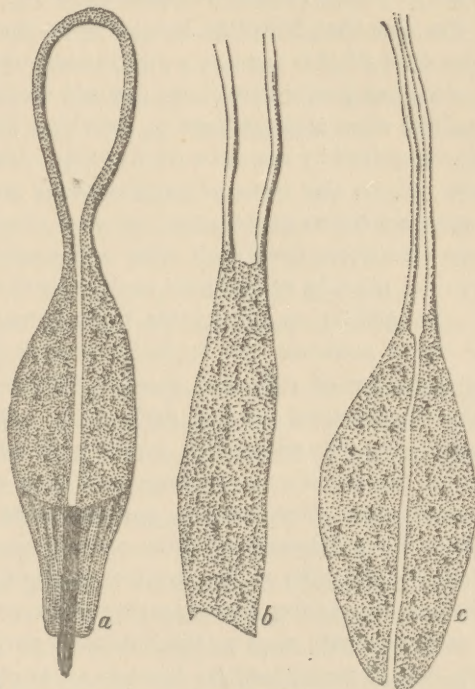
HUMAN RETINA, LAYER OF CONES, X 600 DIAMETERS.



HUMAN RETINA, LAYER OF CONES, $\times 900$ DIAMETERS.

which is some twelve years later, contains a diagram of these twin cones, from which we have taken the accompanying illustration. Notwithstanding the pains he has taken in delineating these structures, he denies the opinion that they are the percipient elements of the retina.

Still later, in 1887, Borysiekiewicz has published a monograph on the structure of the retina as based upon a study of the eyes of lions, tigers, and others of the cat tribe, as well as on the human organ. The illustrations are made with great fidelity to detail, but as they are drawings they are open to criticism, although they agree with the photo-micrographs which are reproduced in this paper. He sums up his treatise by denying that the rods and cones are the end organs of the optic nerve-fibres, and places the percipient elements in the intermediate layers. A brief summary of some of the most important



TWIN CONES (from Hanover.)

physical conditions, which form the basis of our visual perceptions, will materially assist us in understanding the apparatus which is destined to attain this end, and the *modus operandi* of the mechanism which awakens in the brain the recognition of light, form, and color. The simple sensation of light may be awakened by any force acting on the fibres of the optic nerve either at their peripheral endings, or at any point in their course. Such irritation may be purely mechanical, as pressure by the finger on the eyeball, or may be excited by light-waves. The recognition of form requires a certain admixture of light and shadow, or alternately active and passive elements in the retina. The dimensions of these elements on the sensory surface must correspond to the limitations of our perception of form. These elements must also possess within a certain area the same dimensions and a symmetrical arrangement. The size of these elements can be easily calculated. Snellen's standard of visual acuity is based on the perception of lines separated from each other by an angular distance of one minute. The distance of the nodal point of the eye from the retina being 15 mm. (nearly), the

size of such space would be .00435 mm. If we take the experiments of Volkman and others into consideration and reduce the limit to twenty seconds, we obtain a value for the sensitive elements of .00145 mm; we have ourselves obtained such results. The dimensions of the percipient elements would thus be reduced to .00145 mm. This is only one-third of the size that Schultze has given to them. The photo-micrographs show that what is seen as a single cone under a lower power is resolved by a higher power into three distinct elements. It is still necessary to consider what arrangement is provided for restraining the sensory impulse acquired by one cone from communicating itself to the neighboring cone. From the layer of pigment-cells may be seen masses of spongy pigmented tissue penetrating between the separate elements, insulating them effectively from each other and neutralizing all light-waves which have not already spent their energy on the cones.

As Müller and Schultze have already pointed out, no layer of the retina possesses the requisite conditions for these functions excepting the layer of rods and cones. All the other layers have multiple elements situated behind each other; in this layer only is there a single element extending entirely through it. Their regularity of size on the limiting membrane, and their uniform shape, mark them as pre-eminently fitted to the perception of light-waves. Schultze and Müller have determined their measurement to be .0034 to .0036 mm., which would give as the limit of perception an angle of 48". Homogeneous immersion lenses resolve these cones into two or more bodies, as may be easily seen on the left-hand portion of the larger illustration. This would correspond at least to an angle of 24" for limit of perception, which agrees with the result of daily experience. The theory of Henle, Müller, Kölliker, and Pacini, that the rods and cones are the end organs of the fibres of the optic nerve, has been denied by Brücke, Hannover, Borysiekiewicz, and others. Brücke's theory is that the bases of the cones, acting with the pigment-epithelium as concave mirrors, reflect the light back again to the inner layers of the retina, which are thus doubly impressed. Although the twin cones have been long known in the retina of frogs and fishes, it seems never to have awakened the idea of the looped termination being a recurrent nerve-fibre. Hannover, who delineates them so clearly, does not allow them any value as percipient elements. If the sensory impression is made on the bases of the cones by the light which passes through the retina from within outward, its conveyance to the central organ requires that the direction of the force shall be completely reversed. In some way, therefore, we are to find a mechanism which will turn the sensory organs on themselves. Heinrich Müller states that "at times fine fibres sit on the pointed ends of the rods, and are not directed towards the choroid, but are turned inward." Pacini states that the outer end of a rod bends on itself like

a hook, and connects with the end of a cone. In spite of such fidelity in description, the function of these organs still remained obscure.

Light is only conceivable to us as molecular motion. Its perception is only to be explained by the molecular vibration being communicated to the terminal filaments of the nerve-fibres. There is thus a similarity to the other sensations. Our illustrations show that the cones terminate in a looped extremity which passes down over the body of the cone, and, after some convolutions in the position of the so-called external limiting membrane, winds along among the elements of the outer nuclear layer.

Our preparations show a marked difference in the length of the cones, some of them forming their loops much nearer to the external limiting membrane than do others. This can be observed in places where there is no question of mistake by reason of the oblique direction of the section, but where several adjacent cones can be followed throughout their entire length.

We have also seen the terminal loops of the cones distinctly in osmic-acid preparations, but do not present pictures of them because the peculiar color assumed by such retinae renders it difficult to give a good photographic reproduction of them.

A fine longitudinal striation has been observed by many investigators on the bodies of the cones, and the necks of the cones have been seen in the eyes of fishes to possess a series of transverse markings, which presumably was due to their structure being composed of disk-like bodies. In our original photo-micrographs these delicate lines are plainly visible, but reducing the size of the picture has caused them to fade slightly. The longitudinal markings can be traced from nearly the bases of the cones, and are seen to undergo a twisting which on the necks of the cones produces the transverse striations which have previously been described in the eyes of fishes. As the neck recurves and passes down over the body of the cone as a fibre, we can see the portion of the cone over which it passes transversely striated, in some places we thus have transverse and longitudinal markings side by side. The transverse striations do not end in the layer of cones but are plainly visible among the fibres of the outer nuclear layer. They may be followed into the optic nerve by this characteristic spiral wrapping. In the internal granular layer, the investment of the fibres with this covering seems to be reinforced, while other fibres passing at right angles form an arrangement resembling wicker-work. In the layer of optic nerve-fibres a similar arrangement may be observed.

The great difficulty in seeing the looped extremities of the cones arises from the fact that they are buried in the pigment, and when the pigment has been torn off, the ends of the organs are usually mutilated. They are extremely delicate, and even very light pressure of the immer-

sion lens against the cover-glass will cause their complete destruction. It is not possible to follow their outlines through the pigment. We may regard our specimen as very fortunate in the separation of the pigment-epithelium from the extremities of the cones without doing any violence to the structures.

The photo-micrographs were made by artificial light on an 8 x 10 plate. The objective was Reichert's $\frac{1}{15}$ oil immersion. To appreciate minute structure, an extremely narrow pencil of light is necessary. This can be obtained with a mirror at a very oblique angle or, as one of us (Wallace) has found, we can obtain the same result by using a .5 mm. opening in front of our source of light. All the lenses, eye-piece, objective, and condenser should be achromatic. The condenser is varied to suit the amplification, greater amplification requiring lesser area of illumination. It is thus only necessary for 1000 diameters to have the point of light .25 mm. in size in order to cover an 8 x 10 plate. The microscope is used in a horizontal position. A Welsbach's gas-burner, with a sheet-iron chimney, perforated for the diaphragm, furnishes a very satisfactory illumination. The length of exposure for the larger picture was ten hours. This was partly due to the retarding influence of the carmine stain. It will be found best for those who care to use artificial light and homogeneous immersion lenses to let the oil remain on the objective and slide a day or two before photographing and also to let the light burn for an hour before trusting to the focus and centring remaining unchanged during a lengthened exposure.

